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RESEARCH ARTICLE

Visuospatial viewpoint manipulation during full-body illusion modulates subjective first-person perspective

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Abstract Self-consciousness is based on multisensory signals from the body. In full-body illusion (FBI) experiments, multisensory conflict was used to induce changes in three key aspects of bodily self-consciousness (BSC): self-identification (which body 'I' identify with), self-location (where 'I' am located), and first-person perspective (from where 'I' experience the world; 1PP). Here, we adapted a previous FBI protocol in which visuotactile stroking was administered by a robotic device (tactile stroking) and simultaneously rendered on the back of a virtual body (visual stroking) that participants viewed on a head-mounted display as if filmed from a posterior viewpoint of a camera. We compared the effects of two different visuospatial viewpoints on the FBI and thereby on these key aspects of BSC. During control manipulations, participants saw a no-body object instead of a virtual body (first experiment) or received asynchronous versus synchronous visuotactile stroking (second experiment). Results showed that within-subjects visuospatial viewpoint manipulations affected the subjective 1PP ratings if a virtual body was seen but had no effect for viewing a non-body object. However, visuospatial viewpoint had no effect on self-identification, but depended on the viewed object and visuotactile synchrony. Self-location depended on visuospatial viewpoint (first experiment) and visuotactile synchrony (second experiment). Our results show that the visuospatial viewpoint from which the virtual body is seen during FBIs modulates the subjective 1PP and that such viewpoint manipulations contribute to spatial aspects of BSC. We compare the present data with recent data revealing vestibular contributions to the subjective 1PP and discuss the multisensory nature of BSC and the subjective 1PP.

Keywords Bodily self-consciousness · Multisensory integration · First-person perspective · Full-body illusion · Visuospatial viewpoint

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Introduction

Everyday we experience that self and body are bound together. In order to explain how our brain generates this embodied experience, research on the neural underpinning of bodily self-consciousness (BSC) proposed that BSC consists of at least three main aspects: i.e., self-identification, that is the feeling that a particular body is mine, self-location, that is the feeling of where 'I' am located in space, and first-person perspective (1PP), that is the feeling from where 'I' experience the world around me (Blanke and Metzinger 2009; Blanke 2012; Serino et al. 2013).

Research in neurological patients with out-of-body experiences (OBE) has shown that these three phenomenal aspects may be dissociated from the location of the physical body. During an OBE, patients typically experience ownership for an illusory body in external space (abnormal self-identification), they feel their self as elevated above their physical body (abnormal self-location) from where they experience to perceive the world, including their physical body (abnormal 1PP; Blanke and Mohr 2005; Blanke et al. 2002, 2004; De Ridder et al. 2007). In these studies OBEs were linked to the brain's impaired integration of visual, vestibular, tactile, and proprioceptive sensory signals (Blanke et al. 2002; Ionta et al. 2011), suggesting that under normal conditions BSC might be based on multisensory integration mechanisms (Blanke et al. 2004).

Further evidence for this hypothesis came from behavioral experiments in healthy participants that used the so-called full-body illusion (FBI). During one type of FBI, participants received spatially and temporally conflicting sensory information about the location, shape, or size of their body as seen on a head-mounted display. In these studies, participants saw a virtual body from the viewpoint of a camera that filmed the participant's body from behind (2 m distance) and simultaneously received tactile stroking at their physical body (unseen by them) and viewed stroking applied to the back of the virtual body. When stroking was applied in a synchronous fashion participants typically reported increased self-identification and a concomitant bias in self-location toward the virtual body (Lenggenhager et al. 2007; Ehrsson 2007; Guterstam and Ehrsson 2012). These changes in self-identification and self-location were accompanied by changes in visuotactile and audiovisual integration (Aspell et al. 2009, 2010), mental imagery (Lenggenhager et al. 2009; Pfeiffer et al. 2013; Ionta et al. 2011), physiological responses to threat (Petkova et al. 2011; Petkova and Ehrsson 2008; Ehrsson 2007), body temperature (Salomon et al. 2013), and pain responses (Romano et al. 2014; Hänsel et al. 2011). This shows that self-identification and self-location can be experimentally manipulated and that this manipulation modulates cognitive as well as physiological processes regarding the own body.

However, considerably less is known about the multisensory mechanisms underlying the 1PP. Moreover, most research has defined and investigated the 1PP in terms of visual or visuospatial properties, whereas less attention has been given to the multisensory properties of the subjective 1PP, defined as the subjective experience of being directed at the world (Blanke and Metzinger 2009; Metzinger 2003; Ionta et al. 2011; Blanke 2012; Pfeiffer et al. 2013). The former 'perspective' has been defined and investigated as the visuospatial viewpoint of a given visual scene as seen by the participant and thus as centered on the participant's physical body (egocentric viewpoint). This egocentric viewpoint was contrasted with a third-person viewpoint or 'perspective' defined by a visuospatial viewpoint centered at another spatial position of the same scene, but different from the participant's physical body position (allocentric viewpoint; Vogeley and Fink 2003; Vogeley et al. 2004). Insights gained from such explicit visual manipulations of egocentric versus allocentric viewpoints, by task instruction and visual stimulation, provided important insights into processes underlying human social cognition (Aichhorn et al. 2006; Baron-Cohen et al. 1985; Frith and Frith 2003, 2005, 2006), mental spatial transformation (Arzy et al. 2006), and autobiographical memory (Freton et al. 2013). However, it is not known how such viewpoint changes relate functionally and neurally to the perspectival element of BSC: the subjective 1PP.

Ego- and allocentric visuospatial viewpoint manipulations as described above have also been used to investigate their effect on self-identification in a virtual body transfer illusion and the FBI. In an immersive virtual reality experiment, Slater et al. (2010) presented participants with a virtual body and virtual scene as seen from an egocentric (first-person) viewpoint or from a laterally shifted allocentric (third-person) viewpoint. Participants' head movements congruently updated the virtual scenery as seen from each viewpoint, thus providing visuomotor congruency that enhanced the level of immersion. Furthermore, participants received synchronous or asynchronous visuotactile stimulation. Results showed that self-identification ratings and physiological responses (i.e., heart rate deceleration) were higher in the egocentric than allocentric viewpoint conditions and that in the allocentric viewpoint condition stroking additionally modulated these dependent measures of self-identification. In a different study by Petkova et al. (2011), the FBI was induced by presenting to participants either an egocentric or allocentric viewpoint of the abdomen of a mannequin and through additional application of visuotactile stroking (again in synchronous or asynchronous fashion). The authors found that self-identification ratings and physiological responses (here: skin conductance response to threat) were generally higher for egocentric than allocentric viewpoints and that stroking modulated the responses only in the egocentric viewpoint condition. Both Slater et al. (2010) and Petkova et al. (2011) found that self-identification depended on the congruency between the visuospatial viewpoint and the physical body and on viewpoint-dependent effects of visuotactile stroking synchrony. However, whereas visuotactile stroking affected self-identification in the allocentric but not in the egocentric viewpoint condition in the study by Slater et al. (2010), the opposite pattern of result was found in the study by Petkova et al. (2011). Because viewpoint manipulations differed between the studies (e.g., laterally shifted vs. front-facing allocentric viewpoints), it is still unclear which specific visuospatial parameters enable multisensory conflicts (e.g., visuotactile stroking) to induce changes in BSC (e.g., self-identification).

How does the subjective 1PP differ from a mere visual viewpoint from where a scene is perceived? Can changes of the visual viewpoint as tested in these previous studies modulate not only self-identification, but also spatial aspects of BSC such as the subjective 1PP or self-location? Evidence for a dissociation between visual viewpoint and subjective 1PP comes from neurological patients with OBE who reported spatial dissociations between their visual and auditory viewpoints and their subjectively experienced 1PP (Blanke et al. 2004) and also from patients with heautoscopy who alternatingly experienced their subjective 1PP at two distinct visuospatial viewpoints (Brugger et al. 1994; Heydrich and Blanke 2013). De Ridder et al. (2007) for example reported a patient who experienced to see the world from one viewpoint, while experiencing his subjective 1PP and self-location at a different spatial location. This anecdotal clinical evidence about distinct brain mechanisms of visual viewpoint versus the subjective 1PP was corroborated by empirical data in healthy subjects revealing the multisensory mechanisms (tactile, proprioceptive, vestibular, and visual) of the subjective 1PP. This was addressed in two FBI studies that quantified the subjective 1PP as a dependent variable (Ionta et al. 2011; Pfeiffer et al. 2013). In the study by Ionta et al. (2011), participants were presented with visuotactile and visuovestibular conflicts during the FBI. Visuovestibular conflicts consisted of a difference between participant's body posture and the direction of visual gravitational stimuli. Participants lay supine, thus vestibular signals from the otolith organs signaled that the body was facing upwards relative to earth vertical. At the same time, participants saw a video that showed a virtual body in prone posture that was filmed from an elevated location with the camera facing downwards. Thus, vestibular signals (upward direction) and visual signals (downward direction) were in directional conflict. Under these FBI conditions, it was found that half of the experimental participants experienced an upward direction of their subjective 1PP (congruent with vestibular signals), whereas the other half of the participants experienced a downward direction of their subjective 1PP (congruent with visual signals). It was found that participants' judgments of self-location depended on these individual differences in subjective 1PP. These results were replicated by Pfeiffer et al. (2013) in a different subject sample and it was, moreover, found that individual differences in subjective 1PP were congruent with individual differences in visuovestibular integration (as investigated through subjective verticality judgments). Participants with an upward direction of the subjective 1PP (congruent with vestibular signals) were less affected by a visual distractor during subjective verticality judgments, as compared to participants with a downward direction of the subjective 1PP (congruent with visual signals), who were more biased by the visual distractor. Together these results demonstrate that the subjective 1PP was congruent with changes in self-location during the FBI, could be manipulated as a dependent variable between-subjects, and depended on the weighting of visuovestibular signals.

However, it is not known whether systematic changes in the experienced direction of the subjective 1PP can also be induced experimentally within and not just between subjects and whether visual viewpoint manipulations impact the subjective 1PP. Here, we asked whether additionally manipulating visuospatial viewpoints during the FBI could induce within-subject changes of the subjective 1PP and other aspects of BSC (self-location, self-identification). For this, we here repeatedly induced the FBI by robotically supported visuotactile stroking (similar to Pfeiffer et al. 2013) and measured within-subjects the subjective 1PP as the dependent variable. We manipulated the visuospatial viewpoint from which a virtual body was seen on a head-mounted display by combining spatial elevation (high vs. low) with inclination (downward vs. upward) that resulted in two viewpoint conditions: high-downward and low-upward viewpoints. Importantly, participants' body posture and the virtual body posture were not manipulated but were kept constant throughout the experiment. We hypothesized that viewpoint inclination would induce congruent changes of the subjective 1PP. In order to test whether these changes were specific to seeing a human body or would generalize also to non-body objects, we introduced the experimental manipulation Object (body, object) in the paradigm. We hypothesized that during the FBI only seeing a human body and not a non-body object would modulate the subjective 1PP. In a follow-up experiment, we manipulated the synchrony of visuotactile stroking during these viewpoint manipulations in order to link our results from the first experiment to the classical manipulation of BSC during the FBI.

Methods

Participants

In the first experiment, 25 participants were tested (nine females, mean age of 22 years, range of 18–28 years), and in the second experiment, 19 participants were tested (eight females, mean age of 22 years, range of 18–30 years). Participants were students at the Ecole Polytechnique Fédérale de Lausanne, had normal- or corrected-to-normal eyesight, and had no history of neurologic or psychiatric disorder. Participants verbally indicated that they were strongly right-handed. The experimental protocol was approved by the local ethics committee—La Commission d'Ethique de la Recherche Clinique de la Faculté et de Medicine de

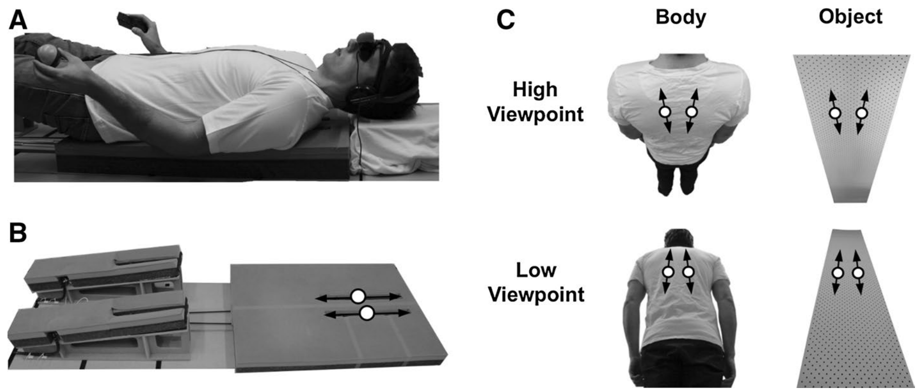


Fig. 1 Experimental setup and stimuli. **a** Participants were lying supine on a robotic device that applied tactile stroking and wore a head-mounted display in which they saw visual stimuli. Responses were given by button press with the *right hand* and participants were holding a ball with the *left hand* to facilitate mental imagery in the mental ball dropping task. **b** Robotic device used for tactile stimulation. Two stroking units (*white circles*) were stroking the back of a participant lying comfortably on soft foam. **c** Visual stimuli showed from a high or low visuospatial viewpoint a virtual human body or a non-body object. Visuotactile stroking consisted of *red dots* (represented here by *white circles*) that moved along the backside of the virtual body or object (*black arrows* represent movement ranges of the dots) and followed the viewpoint-congruent trajectories

l'Université de Lausanne—and was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants gave their informed consent prior to their inclusion in the experiment and after the experiment they were fully debriefed about the experimental purpose and received a monetary compensation of 30 Swiss Francs.

Experimental setup

In a darkened room, a custom-made robotic device was mounted on a table at 90 cm above the floor. Figure 1a, b shows the experimental setup and the robotic device which had 200 cm × 90 cm × 10 cm dimensions and two separate stroking units for tactile stimulation at the back of a participant lying supine on the device (Duenas et al. 2011). Stroking units had 20 cm movement range along a linear trajectory, 2–12 cm/s velocity during stroking and were actuated by ultrasonic motors (Shinsei, USR60-E3N, Japan, http://www.shinsei-motor.com). A plastic sphere was mounted on an elastic blade of the stroking unit, which allowed for adaptation of stroking to participant's back curvature. A soft foam cover on the robotic device allowed participants to comfortably lie supine during the experiment. The foam had gaps allowing the plastic spheres to touch the participant's back. Participants wore a white cotton shirt to reduce frictions between the plastic sphere and their back.

Stroking profiles were programmed in MATLAB software (MathWorks, version R13, http://www.mathworks.ch) and saved in text files that were used to determine robotic stroking paths in LabVIEW software (National Instruments Corporation, version 2010b, www.ni.com/labview).

Visual stimuli were presented to participants on a head-mounted display (HMD, Virtual Realities, Virtual Viewer 3D, www.vrealities.com/virtualviewer3d.html) with a resolution of 800 × 600 pixels, representing about 35° of visual angle. Participants wore headphones that presented white noise to cover the acoustic cues from the movements of the robotic device. In-house software (ExpyVR, http://lnco.epfl.ch/expyvr) was used for visual stimulus presentation, real-time synchronization of visual stroking with robotic stroking, and response recording. Responses were recorded with a serial keypad (Targus Numeric Keypad AKP10US, www.targus.com) on which participants responded with their right hand.

Experimental design

A full-factorial 2 × 2 repeated measures experimental design was used in each experiment. In the first experiment, the experimental factors were Viewpoint (levels: high, low) and Object (levels: body, non-body) resulting in four experimental conditions: (1) high Viewpoint and body Object; (2) high Viewpoint and non-body Object; (3) low Viewpoint and body Object; (4) low Viewpoint and non-body Object (Fig. 1c). In the second experiment, the experimental factors were Viewpoint (levels: high, low) and Stroking (levels: synchronous, asynchronous) resulting in four experimental conditions: (1) high Viewpoint and synchronous Stroking; (2) high Viewpoint and asynchronous Stroking; (3) low Viewpoint and synchronous Stroking; (4) low Viewpoint and asynchronous Stroking.

Stimuli

Visual stimuli were photorealistic images showing a human body (body Object; first and second experiment) or a non-body object of rectangular shape and comparable height and width (non-body Object; first experiment). Both objects were standing upright, i.e., their longitudinal axis was aligned with gravitational vertical. Photos for the stimuli were taken from a fixed eye-to-object distance of 2 m, which was centered on the upper part of the object. The photos were taken from different camera-centered visuospatial viewpoints, as relative to eye level of an average sized observer. Specifically, the photos were taken from 1 m above (or below) eye level and were declined (inclined) by 30° downward to the ground (or upward to the ceiling of the experimental room). All visual cues surrounding the object were then masked by black color to not provide participants with cues about the spatial environment. This resulted in two types of stimuli for the high Viewpoint and low Viewpoint experimental conditions.

Differently to previous studies (Petkova et al. 2011; Slater et al. 2010), all visuospatial viewpoints in the present study were camera-centered and distinct from the viewpoint of the virtual body (allocentric viewpoints). However, because the images were presented to the participant on a head-mounted display and thus the camera viewpoint matched participant's viewpoint, participants perceived the virtual body as if located a few meters in front of them (egocentric viewpoint). Moreover, visual context surrounding the virtual body was removed, such that the viewpoint locations with respect to the external environment were unknown to participants. Thus, a clear definition of our viewpoint manipulations as either egocentric or allocentric seems difficult. Instead, in line with many previous FBI studies, we used camera-centered viewpoints of a virtual body from a distance to induce changes in BSC from the camera viewpoint in the direction of the location and viewpoint of the virtual body (Lenggenhager et al. 2007; Aspell et al. 2009; Ionta et al. 2011; Pfeiffer et al. 2013).

The body object had male gender and was presented to all experimental participants, who were males or females. In order to assess whether gender-mismatch (i.e., male virtual body presented to female participants) had confounded our experimental data, we ran a preliminary analysis of our data consisting of including a between-subjects factor Gender in all ANOVAs laid out in the 'Analysis' section. Results showed no gender-related main effects or interactions (all F values <1), suggesting that gender-mismatch did not affect our data, and we therefore decided to include all data from all participants in subsequent statistical analysis.

In addition to visuospatial viewpoint, we manipulated the synchrony of visuotactile stroking (second experiment) in order to be able to compare our results to previous studies on the FBI. Visual stroking consisted of virtually augmenting two red dots on the back of the virtual body/object and moving them along pre-defined stroking sequences (Fig. 1c, black arrows indicate the movement range of the red dots). Visual stroking was applied along a movement range that was centered on the virtual body/object; the motion of the red dot corresponded to the visuospatial viewpoint manipulation. Specifically, a downward stroke along the virtual body/object was visually seen in the high (low) Viewpoint condition as two red dots converging (diverging) and decreasing (increasing) in size and thus followed congruently the anatomy of the virtual body/object (Fig. 1c, see difference in orientation of black arrows in high and low viewpoint condition). Tactile stroking consisted of moving two plastic spheres along the back of the participant lying on the robotic device (Fig. 1a, b).

The sequences of visual stroking (seen on the HMD) and tactile stroking (felt on participant's back) were either synchronous (first and second experiment) or asynchronous (second experiment). Two stroking profiles were created before the experiment. Each profile consisted of a random sequence of positions in 0–20 cm distance range, 2–12 cm/s velocity range, and 40 s duration. The stroking profiles varied randomly in length, speed, direction, and inter-stroke-intervals (0–1.5 s). Thus, when different profiles were simultaneously executed they were spatially incongruent. During the experiment, either twice the same profile or both incongruent profiles were randomly assigned to the red dots (seen on the HMD) and the stroking units (touching the back of the participant), which resulted in synchronous or asynchronous visuotactile stroking.

Measures of bodily self-consciousness

Subjective 1PP was measured by presenting to participants on the HMD the phrase 'Orientation?' in white on black background along with the words 'upward' and 'downward' at the left and right bottom of the screen. Participants were trained to rate by button press their experienced direction of the subjective 1PP according to the question 'Did you have the impression as if you were looking upward/downward at a body/object above/below you?'. Participants responded with two alternative forced choices using either the right index finger for rating 'upward' (coded 0) or the right middle finder for rating 'downward' (coded 1).

Self-location was measured using the mental ball dropping (MBD) task, which has previously been shown to be a sensitive measure of self-location (Lenggenhager et al. 2009; Ionta et al. 2011; Pfeiffer et al. 2013). The MBD task was performed in three sequential steps: First, participants imagined to drop a ball from their hand upon which they pressed a button with their right index finger; secondly, they imagined the ball falling toward the ground during which they held the button depressed; finally, participants imagined the ball hitting the ground upon which they released the button. The duration of button press (response time, RT) was used as a measure of self-location (i.e., height) above the ground. Note that participants were familiarized with the task procedure before the experiment and performed at least 20 repetitions of the MBD task before the experiment.

Self-identification, along with other items on illusory touch and other self-related experiences, were rated in the FBI questionnaire (Lenggenhager et al. 2009; Pfeiffer et al. 2013). Figure 3c lists all items of the questionnaire. The questionnaire inquired about the quality of the FBI experience and each question was presented separately on the screen in white color on black background in the center of the screen along with a visual analogue scale, i.e., a horizontal and continuous visual scale with 11 levels. Questions were presented in random order; participants had no time limits to answer each question and gave their ratings by navigating a mouse curser along the visual analogue scale. Questions had an 11-point scale that ranged from 1 ('weak feeling') to 11 ('strong feeling').

Procedure

Each of the four experimental conditions was repeated 15 times in random order. The total of 60 experimental trials was presented in three separate runs of 20 trials. Between runs participants were allowed pauses in lying posture on the robotic device.

An experimental trial began with presenting visuo-tactile stroking for 40 s. Participants were instructed to attend simultaneously to the visual stimulation (seen on the HMD) and the tactile stimulation (felt on the participant's back). Immediately after that, tactile stroking stopped and all visual stimuli were removed from the HMD and a black screen was shown for 1 s. Then, an auditory beep sound was presented for 200 ms, cueing participants to perform a MBD task within 6 s (adapted from Lenggenhager et al. 2009; Ionta et al. 2011; Pfeiffer et al. 2013), this procedure was repeated three times resulting in three repeated measures of MBD RTs. After that, participants rated their subjective 1PP by button press within 6 s. Then a fixation cross was presented on the screen during a resting phase of 15 s before the next trial began.

After having completed the FBI experiment on the robotic device, participants were comfortably seated in front of a computer screen on which they rated the FBI questionnaire separately for each of four experimental conditions. Between subjects, the order of condition-wise questionnaire administration and the order of question were randomized. There was no time limit to complete the questionnaire ratings.

Analysis

After having recorded raw data from all participants, the data were pre-processed and condition-averages were calculated.

Subjective 1PP ratings were processed by calculating proportion scores by dividing the number of 'downward' ratings by the number of total ratings for each condition. Omitted responses (<5 % per subject) were excluded from this analysis. Proportion scores indicated the proportion of having rated 'downward' in each experimental condition and ranged from 0 (never rated 'downward') to 1 (always rated 'downward').

Response times (RTs) from the MBD task (i.e., measure of self-location) were processed by removal of omissions and RTs shorter than 200 ms (<5 % per subject), which is considered too short for this type of mental imagery (Pfeiffer et al. 2013; Lenggenhager et al. 2009). First, we calculated trial-average RTs across three subsequent repetitions of the MBD task and then calculated condition-average RTs for each participant.

FBI questionnaire ratings were recorded separately for four experimental conditions with each 10 questions. In order to account for response tendencies of participants, e.g., general (dis-)agreement to all questions or generally using extreme ends of the scale, that might have confounded the interpretation of questionnaire data, we transformed the data to ipsative scores (Broughton and Wasel 1990; Cattell 1944). Ipsative normalization was performed within-subjects and consisted of calculating across all questions the average score and the standard deviation of scores. Then, each rating was centered (i.e., subtracting the average score) and normalized (i.e., divided by the standard deviation). Ipsative scores reflect agreement (i.e., positive values) or disagreement (i.e., negative values) relative to the average response of the participant across all questions (i.e., zero value), where each unit reflects a standard deviation agreement (+1) or disagreement (−1) with questionnaire item. This procedure resulted in condition-wise ipsative scores for each question.

Condition-average subjective 1PP ratings and RTs from the MBD task were statistically analyzed using separate 2 × 2 repeated measures ANOVAs. For proportion scores of 1PP and RTs for self-location, we applied an a priori alpha level threshold of .05. Post hoc comparisons were performed for significant interactions from the ANOVA and thus an alpha level threshold of .05 was used—uncorrected for multiple comparisons. Questionnaire data of 10 questions were analyzed using separate 2 × 2 repeated measures ANOVAs for each of the questions. We corrected for multiple comparisons using Bonferroni correction (Bonferroni 1935), which resulted in an alpha level threshold of .005.

Results

Experiment 1

Subjective 1PP

Statistical analysis revealed a main effect of Viewpoint ($F(1, 24) = 10.80$, $p = .003$, $\eta^2 = .31$; Fig. 2a), reflecting more frequent 'downward' 1PP for high Viewpoint ($M = .64$, SE = .06) than for low Viewpoint ($M = .32$, SE = .05), which shows congruency between 1PP ratings and visual viewpoint inclination (see 'Stimuli' section). Critically, we also found a significant Viewpoint × Object interaction ($F(1, 24) = 8.22$, $p = .008$, $\eta^2 = .26$; Fig. 2a), reflecting that when participants were presented with a virtual body they rated to have experienced a 'downward' direction of the 1PP more frequently in the high Viewpoint condition ($M = .75$, SE = .07) compared to low Viewpoint condition ($M = .21$, SE = .05) (post hoc paired-samples t test: $t(24) = 5.16$, $p < .001$). Instead, when presented with a non-body object, participants rated the subjective 1PP not differently between high Viewpoint ($M = .53$, SE = .07) and low Viewpoint ($M = .44$, SE = .08; post hoc paired-samples t test: t value < 1). These results suggest that the effects of the visuospatial viewpoint on the subjective 1PP are body-specific.

Self-location

Statistical analysis of MBD RTs showed a marginally significant main effect of Viewpoint ($F(1, 24) = 4.17$, $p = .052$, $\eta^2 = .15$; Fig. 2b) with slightly higher self-location for high Viewpoint ($M = 926$ ms, SE = 41 ms) than for low Viewpoint ($M = 914$ ms, SE = 41 ms). Thus, self-location showed a difference in height estimation congruent with the viewpoint elevation manipulation. There was no main effect of Object and no Viewpoint × Object interaction (all F values <1). Together these results suggest that visuospatial viewpoint tended to affect self-location independently of whether a body or non-body object was shown. Note that all experimental conditions were presented in synchronous visuotactile stroking, which typically induces self-location changes in the direction of the seen virtual body during the FBI (Ionta et al. 2011; Lenggenhager et al. 2009).

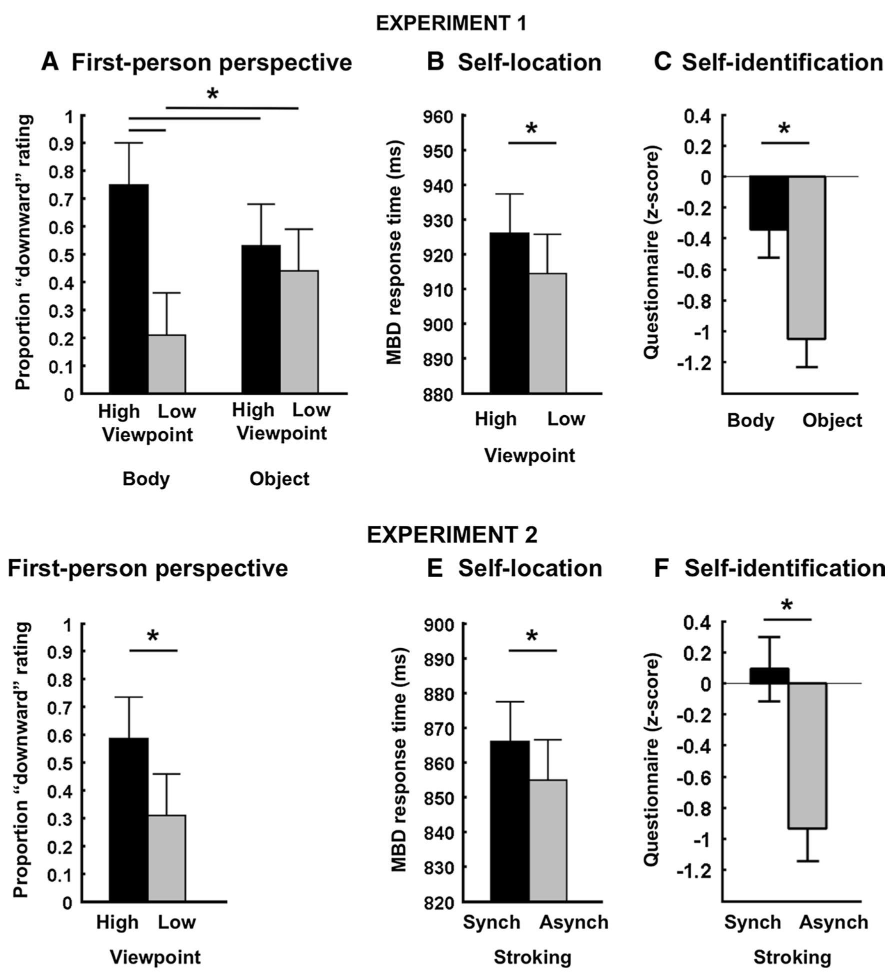
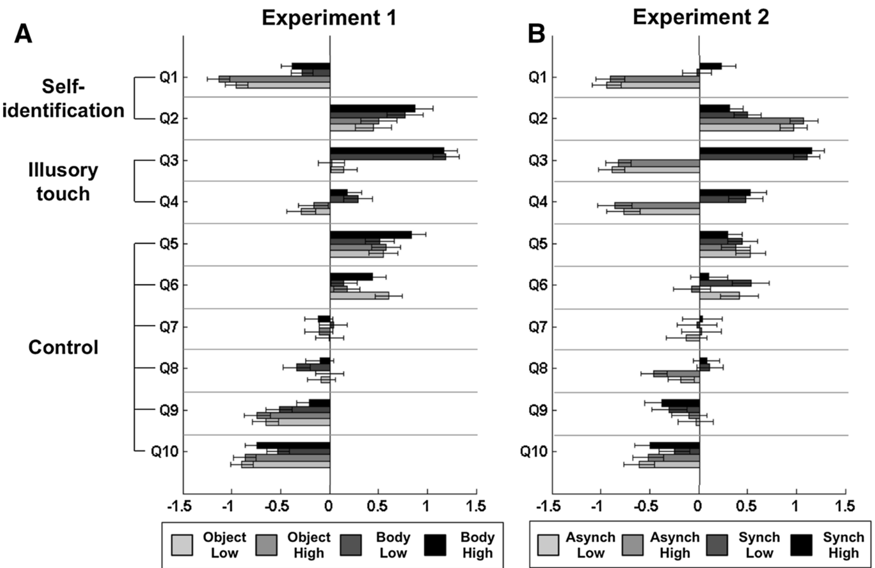


Fig. 2 Results from Experiment 1 (**a–c**) and Experiment 2 (**d–f**) for subjective 1PP ratings (**a, d**), RTs of the MBD task, our measure of self-location, (**b, e**) and questionnaire ratings for self-identification (**c, f**). *Error bars* in all plots show 95 % confidence intervals of within-subjects interaction variance from the repeated measures ANOVA (Loftus and Masson 1994)



C

1. How strong was the feeling that the body you saw was you?
2. How strong was the feeling that you were looking at someone else?
3. How strong was the feeling that the touch you felt was located where you saw the stroking?
4. How strong was the feeling that the red dot you saw was directly touching you?
5. How strong was the feeling that you were located at some distance behind the visual image of the body that you saw?
6. How strong was the feeling that you were drifting downwards or upwards?
7. How strong was the feeling that you had more than one body?
8. How strongly did you feel the touch simultaneously at two locations in space?
9. How strong was the feeling to float in the air?
10. How strong was the feeling that you were dissociated from your body (as if your self and your body were in different locations)?

Fig. 3 Questionnaire results summarized. **a–b** Ipsative scores for all questions (*y*-axis) as a function of experimental conditions (*shades of gray*) indicate participants average responses by a value of zero and agreement (+) and disagreement (−) in standard deviation units. *Error bars* show 95 % confidences intervals. **c** Questions of the FBI questionnaire

FBI questionnaire

Figure 3a summarizes the questionnaire results. FBI questionnaire score analysis revealed a significant main effect of Object for self-identification (Q1: $F(1, 24) = 19.39$, $p < .001$, $\eta^2 = .45$; Fig. 2c), reflecting higher scores for the body Object condition ($M = -.34$, SE = .14) than the non-body Object condition ($M = -1.05$, SE = .09). We also found a main effect of Object for illusory touch (Q3: $F(1, 24) = 31.90$, $p < .001$, $\eta^2 = .57$) showing higher scores for the body Object condition ($M = 1.17$, SE = .16) than the non-body Object condition ($M = .07$, SE = .17). No further questions showed a significant main effect of Object, and there were no main effects of Viewpoint and no viewpoint × object interaction. Together these results suggest that during synchronous visuotactile stimulation, self-identification and illusory touch increased when stroking was visually presented on a virtual human body as compared to a non-body object. These results likely reflect effects of top-down knowledge about body-identity on self-identification and illusory touch.

Summary of results

Our results showed that manipulating participants' visuospatial viewpoint and the identity of the visual stimulus during the FBI affected three components of BSC. In particular, visuospatial viewpoint had a specific effect on self-location, but not on self-identification as measured through questionnaire scores: Participants localized themselves toward a higher location in the high Viewpoint conditions. Conversely, object identity selectively affected self-identification and, in line with previous studies, self-identification was rated higher when a virtual body was presented as compared to a non-body object (Lenggenhager et al. 2007; Aspell et al. 2009). Finally, only the experienced direction of the 1PP was affected by the combination of the two factors and visuospatial viewpoint effects on subjective 1PP were specific to seeing a virtual body, but absent for the non-body object.

Experiment 2

Subjective 1PP

Statistical analysis revealed a main effect of Viewpoint ($F(1, 18) = 5.91$, $p = .026$, $\eta^2 = .25$; Fig. 2d), reflecting more frequent 'downward' 1PP for high Viewpoint ($M = .59$, SE = .08) than for low Viewpoint ($M = .31$, SE = .06). These results are consistent with results from experiment 1. The analysis showed no main effect of

Stroking and no Viewpoint × Stroking interaction (all F values <1).

Self-location

Statistical analysis of MBD RTs showed a main effect of Stroking ($F(1, 18) = 6.44$, $p = .021$, $\eta^2 = .26$; Fig. 2e) with higher self-location for the synchronous Stroking ($M = 866$ ms, SE = 51 ms) than for the asynchronous Stroking conditions ($M = 855$ ms, SE = 50 ms). These results show that the self-location drifted upwards toward the image of the virtual body (shown in the HMD) and was thus corresponding to the direction of participants' body posture lying on the back. However, there was no main effect of Viewpoint and no viewpoint × stroking interaction (all F values <1). These results suggest that visuospatial viewpoint had no effect on self-location, but that self-location drifted independently of viewpoint in an upward direction congruently with participants' body orientation on the robotic device.

FBI questionnaire

Figure 3b summarizes the questionnaire results. Questionnaire score analysis revealed a significant main effects of Stroking for questions inquiring about self-identification (Q1: $F(1, 18) = 32.61$, $p < .001$, $\eta^2 = .64$; Q2: $F(1, 18) = 12.87$, $p = .002$, $\eta^2 = .42$; Fig. 2f) and illusory touch (Q3: $F(1, 18) = 112.10$, $p < .001$, $\eta^2 = .86$; Q4: $F(1, 18) = 29.21$, $p < .001$, $\eta^2 = .62$). The two questions concerning self-identification showed a consistent result: Self-identification with the virtual body (Q1) was rated higher for synchronous ($M = .09$, SE = .18) than asynchronous Stroking ($M = -.94$, SE = .14), and identifying the virtual body as being somebody else (Q2) was rated higher for asynchronous ($M = 1.00$, SE = .22) than synchronous stroking ($M = .39$, SE = .23). Both questions on illusory touch were rated higher for synchronous (Q3: $M = 1.11$, SE = .11; Q4: $M = .49$, SE = .23) than asynchronous Stroking (Q3: $M = -.87$, SE = .17; Q4: $M = -.83$, SE = .15). These results are consistent with previous FBI studies using a variety of different stimulation and virtual reality protocols (Ehrsson 2007; Lenggenhager et al. 2007, 2009; Petkova et al. 2011). None of the questions that are generally given as control questions in the FBI (Q5–Q10) showed significant main effects or interactions. Subjective 1PP, in addition to trial-wise ratings, was also rated in the FBI questionnaire. Notably, no question showed a main effect or interaction with Viewpoint, thus neither self-identification ratings (Q1, Q2), nor illusory touch ratings (Q3, Q4) were affected by visuospatial viewpoint (all p values >.5).

Discussion

Within-subject manipulation of subjective 1PP

We found that within-subjects subjective 1PP changed congruently with our visuospatial viewpoint manipulations, although the physical body of our participants was upward-directed in supine posture throughout all experiments. Participants experienced a downward-directed 1PP more often when they saw a virtual body from a downward-directed viewpoint than from an upward-directed viewpoint. Notably, these changes were obtained by repeated measurements within-subjects and agree with the phenomenology of OBEs of neurological origin. Patients often experience disembodied downward-directed 1PP while their physical body is upward-directed in supine posture (Blanke et al. 2002, 2004; De Ridder et al. 2007). Our results also extend previous FBI studies in healthy individuals (Pfeiffer et al. 2013; Ionta et al. 2011) where downward-directed viewpoints were used to induce visuovestibular conflict about the direction of constant gravitational acceleration. These manipulations induced between-subjects changes of the subjective 1PP (i.e., in terms of the experienced direction of the 1PP). In the present study, downward- and upward-directed visuospatial viewpoint manipulation induced congruent changes of the subjective 1PP within-subjects. Our data indicate that visuospatial viewpoint manipulations are more powerful in altering the subjective 1PP across subjects when compared to visuovestibular conflicts used in previous studies (Pfeiffer et al. 2013; Ionta et al. 2011).

Body-specific manipulation of subjective 1PP

In the present study, subjective 1PP was modulated by viewpoint only when a virtual human body was presented, but not for a non-body object. This body-specific effect was found during ongoing synchronous stroking that is known to induce self-identification with the virtual body, but not a non-body object as in previous FBI studies (Lenggenhager et al. 2007; Aspell et al. 2010; Petkova and Ehrsson 2008).

Similar body-specific effects have previously been described in related studies on BSC. For example, the rubber hand illusion is abolished when a non-body object instead of a fake hand is shown (Tsakiris and Haggard 2005). Similarly, a body-shaped object, such as a mannequin, but not a non-body object, allows inducing the FBI (Aspell et al. 2009; Lenggenhager et al. 2007). Brain imaging work has shown that a network of posterior brain regions is highly tuned to extract the visual shape of body parts or whole bodies, for example in the extrastriate body area in the lateral occipital cortex (Kanwisher et al. 1997; Astafiev et al. 2004; Gentile et al. 2013). This literature also provides evidence that visual processing of the body (or face) depends on the spatial orientation of the image (de Gelder et al. 2010; Minnebusch and Daum 2009 for reviews). This has been tested by the body/face inversion effect, consisting in RT or neural activation differences for visual processing upright versus inverted body or face (but not object) stimuli. The body inversion effect gradually depends on the angular deviation magnitude between upright and rotated image (Minnebusch et al. 2010). Accordingly, our visual body stimuli differed in the rotational tilt of the body stimulus with respect to the camera viewpoint (Fig. 1c). Based on the previous literature, it seems plausible that the body processing brain network encoded orientation differences of the virtual body (but not the non-body object) and that therefore subjective 1PP ratings depended on information encoded in the body processing network.

Other studies have shown that vision of bodily shapes is relevant to multisensory integration and seeing one's own body enhances touch processing (Kennett et al. 2001) and reduces tactile pain (Longo et al. 2012) as compared to seeing a non-body object. In addition to that, these body-specific effects on the subjective 1PP show that global visual features alone cannot induce these changes, but that more detailed visuospatial information is required. Specifically, in both body and object conditions, global visual features were identical. Thus, the location where the visual perspectival lines converged on the display was identical, i.e., for high viewpoint the lines converged in the lower part of the screen, whereas for low viewpoints the lines converged in the upper part of the screen. Yet subjective 1PP was modulated differently by the visual viewpoint only in the body condition.

Subjective 1PP and visuospatial viewpoint

Our results showed that subjective 1PP ratings (i.e., upward, downward) depended on the visuospatial viewpoint inclination angle (i.e., upward for low viewpoint, downward for high viewpoint) when a virtual body was seen. This suggests that visuospatial viewpoint information is highly relevant to subjective 1PP experience.

Are subjective 1PP ratings more than judgments of visual features of the experimental stimuli? This is indeed suggested by the absence of viewpoint effects on subjective 1PP ratings when a non-body object was seen, i.e., subjective 1PP ratings were at chance level for both viewpoint conditions when a non-body object was shown (see Fig. 2a). Furthermore, visual judgments would have led to extreme values for subjective 1PP ratings (i.e., 0 or 1 proportion of downward 1PP rating). This was not observed, rather, for each participant subjective 1PP ratings ranged between .2 and .9 proportion per experimental condition, which is also reflected in the group average proportions ranging in Experiment 1 from .2 to .75 proportion downward rating (Fig. 2a) and in Experiment 2 from .3 to .6 proportion downward rating (Fig. 2d). Furthermore, in a previous FBI study, we presented the same downward-directed visuospatial viewpoint to all participants but observed individual differences in subjective 1PP ratings depending on visuovestibular integration and furthermore found within-subjects modulation of subjective 1PP ratings by visuotactile stroking (Pfeiffer et al. 2013). We note that two perceptual interpretations of our visual stimuli were possible. Participants may have either experienced viewing the scene from a fixed camera viewpoint and a virtual body in front of them at different rotational tilt angles or they may have experienced viewing a virtual body at a fixed spatial orientation from differently tilted camera viewpoints. Whereas the former experience (i.e., fixed viewpoint) should have decreased variance in 1PP ratings across conditions, the latter experience (i.e., fixed virtual body) could have been associated in viewpoint-dependent changes of 1PP ratings as observed in our experiments. However, our study did not directly address this issue and further studies should directly address this issue. Together, the present and the previous results show that in healthy subjects during the FBI subjective 1PP ratings depend on visual, vestibular, and tactile signals. Furthermore, visuospatial viewpoint information is highly relevant to subjective 1PP ratings, but only if a virtual body is seen.

Subjective 1PP: no modulation by visuotactile stroking

Results from the second experiment showed no effects of visuotactile stimulation on the subjective 1PP. This observation differs from previous data showing that asynchronous stroking induced more frequent 'downward' 1PP ratings than synchronous stroking (Pfeiffer et al. 2013). However, different degrees of visuovestibular conflict were used in these studies, i.e., 180° directional conflicts were used in the study by Pfeiffer et al. (2013) and 90° directional conflicts were used in the present study. Thus, multisensory—visual, tactile, and vestibular—signals seem to determine the subjective 1PP. Moreover, we note that visuotactile stimuli related to the stroking manipulation were uninformative about the spatial configuration of the virtual body and the participant's body with respect to the external environment. That is, in all experimental conditions, visual stroking (i.e., red dots) and tactile stroking (i.e., touch at the back) were applied to the back of the virtual body and participant's body and were seen from 2-m distance. The observation that visuotactile stroking in the present conditions does not modulate the subjective 1PP raises the question which combinations of multisensory visual-tactile-vestibular stimulus combinations most strongly affect the subjective 1PP. Previous behavioral and psychophysics studies have provided evidence that the perception of the spatial orientation of the own body in space is affected, for instance, by footsole pressure (Lackner 1992; Lackner and DiZio 2000), neck-muscle vibration (Lackner and DiZio 2005), large-field optokinetic stimulation (De Saedeleer et al. 2013), or static tilts of the visual environments (Tiliket et al. 1996). These multisensory effects on spatial perception suggest that similar stimulations may also impact spatial aspects of BSC, in particular the subjective 1PP.

Subjective 1PP relationship to self-location

In addition to the effects on 1PP, our results showed that self-location was affected by viewpoint. In the first experiment in the elevated viewpoint condition, subjects judged themselves to be higher above the ground, whereas the lowered viewpoint was associated with self-location that was closer to the ground. Thus, self-location and 1PP were similarly affected by viewpoint. Associations between 1PP and self-location were also found previously between-subjects during visuovestibular conflict (Ionta et al. 2011; Pfeiffer et al. 2013). The present study shows congruency between subjective 1PP and self-location only in these conditions and not related to stroking or for the non-body object.

We argue that the absence of an association between 1PP and self-location in the present study may be explained by the fact that weak and constant visuovestibular conflicts were employed and thus the present study differed from the results of previous studies where strong visuovestibular conflicts were presented (Pfeiffer et al. 2013; Ionta et al. 2011). More precisely, in the present experiment the visuovestibular conflict (between the visual gravity cues of the virtual body and the vestibular cues of the participant's body) were less strong. There was only a 90° visuovestibular angle difference in the present study, whereas (Ionta et al. 2011) employed a conflict of 180°. Here, we manipulated the visual viewpoint, thus the visuospatial representation showed less consistent effects on self-location, but more consistent effects on 1PP.

Self-identification: no modulation by visuospatial viewpoint

Self-identification with a virtual body depended on the synchrony between stroking felt on one's own body and seen on the avatar's body, self-identification was stronger when seeing a virtual body, and independent of the participant's visuospatial viewpoint manipulation. We found in the first experiment higher self-identification with a virtual body than a non-body object when stroked synchronously, and in the second experiment, higher self-identification ratings for synchronous than asynchronous stroking. Our results confirm previous bodily illusion studies that manipulated the synchrony of visuotactile stroking or tapping on virtual or fake hands (Botvinick and Cohen 1998), faces (Sforza et al. 2010; Tsakiris 2008), or whole bodies (Ehrsson 2007; Lenggenhager et al. 2007). Our results also agree with the previous studies showing body-specific effects of stroking for fake hands (Tsakiris and Haggard 2005) and whole bodies (Lenggenhager et al. 2007; Aspell et al. 2009). Together, the present results confirm that low-level cues in multisensory stimuli, such as temporal synchrony, as well as high-level body shape information, are processed by the central nervous system to generate self-identification with the whole body. Furthermore, our results show that our manipulations of viewpoint did not prevent or modulate the induction of the FBI and that using well-controlled robotic stroking and virtual reality can be used to manipulate self-identification with a virtual body.

However, viewpoint manipulation did not affect self-identification in both our experiments and this seems to contradict viewpoint effects reported in the study by Slater et al. (2010) for virtual body transfer and by Petkova et al. (2011) for the FBI. These studies did find that different visuospatial viewpoints affected subjective ratings of self-identification and objective measures, such as heart beat and skin conductance response. However, these authors manipulated egocentric versus allocentric visuospatial viewpoints and thus compared the effects of extracorporal (third-person) and body-centered (first-person) viewpoints. On the contrary, in the present study, we compared two allocentric, i.e., two extracorporeal, viewpoints, and then we measured their effects on different aspects of BSC.

In other words, the studies by Slater et al. (2010) and Petkova et al. (2011) compared a visuospatial viewpoint that was embodied within a virtual body with a disembodied viewpoint (as seen from a distance) from a virtual body, reporting stronger self-identification for embodied versus disembodied viewpoints. In our study, we compared two disembodied viewpoints that differed in terms of the elevation along the vertical axis. Using the same distance between both disembodied viewpoints from the virtual body, our viewpoints were either elevated-downward directed or lowered-upward directed. Therefore, our results do not contradict, but rather extend the results by Slater et al. (2010) and Petkova et al. (2011) by showing that self-identification with a virtual body from a distance does not depend on elevation or direction of viewpoint, but can be achieved under different visuospatial conditions.

Conclusion

Manipulating the visuospatial viewpoint elevation level above the ground from which healthy participants observed a humanoid virtual body induced congruent changes of the experienced direction of the subjective 1PP. Similar manipulation of visuospatial viewpoints for observing a non-body object did not modulate subjective 1PP experience, indicating that visuospatial viewpoints affected the subjective experience at what ‘I’ am directed (i.e., subjective 1PP) only if a humanoid body shape was seen. Visuospatial viewpoint manipulations had no effects on self-identification with a virtual body, which rather depended on visuotactile stroking synchrony. Thus, subjective 1PP and self-identification depended on different sensory stimulation parameters, suggesting potentially distinct underlying neural representation. Together, our results provide evidence for a close relationship between visual processing of body shape and visuospatial viewpoints contributing to spatial aspects of BSC. Furthermore, our results extend previous studies by demonstrating for the first time that within-subjects manipulation of subjective 1PP is malleable. More generally, our study showed that combining virtual reality, robotics technology, and cognitive neuroscience experimental approaches can further our understanding of the neurobiological basis of self-consciousness.

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